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THE MORPHOLOGY OF THE PETROSAL BONE AND OF THE SPHENOIDAL REGION OF THE SKULL OF AMIA CALVA.

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THE sphenoidal region of the skull of vertebrates is that part of the base and sides of the skull that corresponds to that part of the skull of man that is occupied by the sphenoid bone. This bone in man (No. 24, vol. ii, pt. i) lies between the ethmoid bone anteriorly and the occipital and temporal bones posteriorly, and has two portions,— an anterior, presphenoidal part, and a posterior, postsphenoidal part. The presphenoidal part of the bone contains a median element, the presphenoid, and two lateral elements, the orbitosphenoids, one on each side of the head. The postsphenoidal part of the bone contains a median element, the basisphenoid, and three lateral elements on each side, the alisphenoid, the sphenotic, and the internal pterygoid plate, the latter being developed from one of the appendages of the skull, the palatopterygoid bone, and hence not a part of the cranium proper.

The presphenoid first appears in man, according to Sutton (No. 29, p. 581), as a pair of nuclei on the inner sides of the optic foramina. These nuclei lie on the deep aspect of the perichondrium, and do not involve the subjacent cartilage

until they have attained some considerable size. They fuse first with the orbitosphenoids; then with each other, by sending a thin shell of bone across the dorsal aspect of the cartilage that separates them; and then with the basisphenoid. Much later they fuse with each other in the deeper parts of the separating cartilage.

According to Thane (No. 24, vol. ii, pt. i, p. 76) the presphenoid of man may develop from the two nuclei of Sutton, or may be "an independent growth." This latter possibility is perhaps of some considerable morphological importance, as will be later seen.

The basisphenoid first appears as two nuclei in the cartilage forming the floor of the pituitary fossa (No. 29, p. 580), that fossa being the sella turcica of the adult (No. 24, vol. ii, pt. i, p. 75).

In Amia the prefrontals of Sagemehl's descriptions and my own are the lateral ethmoids, or ectethmoids of English writers, the generally accepted homologues of the lateral masses of the ethmoid bone of man; and the petrosals are the prootics, the generally accepted homologues of the correspondingly named parts of the petrous part of the temporal bone of man. The sphenoidal region of the skull of Amia would accordingly be, if the bones alone were considered and the homologies implied in their names accepted, that part of the base and sides of the skull that lies between the prefrontals anteriorly and the basioccipital, squamosals, and petrosals posteriorly.

The region so defined in Amia contains, on each side of the head, four primary ossifications, three of which are called by Sagemehl (No. 25) the orbitosphenoid, alisphenoid, and postfrontal; while the fourth is considered by him as one half of a basisphenoid bone. The postfrontal of this nomenclature is the sphenotic of Bridge's descriptions of Amia (No. 7), and the postorbital ossification of my own (No. 1, p. 479).

The orbitosphenoid (No. 2, Figs. 8–11) lies between the orbito-nasal fenestration (No. 2) of the optic wall of the skull and the optic fenestra (No. 25, p. 202); the alisphenoid between the latter fenestra and the two trigeminal foramina. The orbito-nasal fenestra lies, in larvae of Amia, and hence

morphologically in the adult also, in front of the foramen by which the olfactory nerve leaves the cranial cavity. The optic fenestra is, according to Sagemehl, simply the greatly enlarged foramen of the nervus opticus, but it includes, in its posterior portion, as will later be shown, the tall orbital opening of my descriptions of the eye-muscle canal (No. 2), which opening transmits the oculomotorius, trochlearis, profundus, and abducens nerves, and is the fused foramina of those nerves and that of the vena ophthalmica (No. 2).

The orbitosphenoid and alisphenoid, both of which form parts of the side wall of the skull, thus lie respectively between the olfactory and profundus nerves, and the profundus and trigeminus. Posterior to the alisphenoid the petrosal occupies a similar position between the facialis and glossopharyngeus.

The profundus, trigeminus, facialis, and glossopharyngeus are all generally considered as segmental nerves; the olfactorius is sometimes so considered (Nos. 6, 18); and Marshall suggests (No. 18, p. 38) that the opticus also may possibly be of segmental value.

The orbitosphenoid, alisphenoid, and petrosal bones of Amia thus have, in general position, the same relation to segmental nerves that the several components of the occipitale laterale have (No. 2). This markedly interneural, and hence segmental or intersegmental, whichever it may be, position of the bones in Amia, thus gives no support whatever to Vrolik's conclusion (No. 32, pp. 240, 251) that the occipitale laterale and petrosal of fishes are ossifications of the side wall of the brain case, formed, respectively, around the vagus and facial foramina. The alisphenoid would naturally, under Vrolik's interpretation of the bones, be an ossification formed around the trigeminal foramina.

The postfrontal of Sagemehl, my postorbital ossification, forms part of the dorso-lateral edge of the skull in the region between the trigeminus and facialis.

The two so-called halves of the basisphenoid lie in the base of the skull in the region between the olfactorius and profundus, if not perhaps between the opticus and profundus.

In teleosts, in marked distinction to Amia, the basisphenoid is a single median bone. It is, moreover, a most inconstant element of the teleostean skull. According to Vrolik (No. 32, p. 276) it may be found in connection with an eye-muscle canal, or where that canal does not exist; there may be an eye-muscle canal and no basisphenoid, or neither eye-muscle canal nor basisphenoid; the bone may, in some fishes, be replaced by a ligament; and in still others it may be fused with the parasphenoid, and appear as a median, vertical process of that bone. It is said by Vrolik (No. 32, p. 254) to develop in Salmo as two lateral T-shaped nodules, which later fuse to form the single impair bone.

In all descriptions that I find of it, it lies between the extreme hind ends of the orbits and gives attachment and support to, or forms part of, the hind edge of a more or less developed membranous, ventral portion of the interorbital wall or septum. It may be preformed in cartilage (No. 32, p. 247), or it may develop wholly or in part in that membranous part of the interorbital septum to which it is destined later to give support (No. 32, pp. 254, 259, and No. 20, p. 139). In this latter case, in the single instance cited, the salmon, both Vrolik and Parker say that the interorbital septum itself is at first formed entirely of membrane, which later becomes invaded by cartilage.

The membranous portions of the interorbital region of the skull of Salmo, and hence of other fishes also, thus seem to represent simply an arrested condition in the development of the side walls of the cartilaginous cranium. Such being the case, the teleostean basisphenoid and orbitosphenoid, both of which develop either in the interorbital membrane or in the cartilage which may replace it, must be of primary, and not of secondary origin; and they would not necessarily cease to be strictly homologous with the corresponding bones in higher vertebrates, as Vrolik definitely says they do (No. 32, p. 259), simply because of their histologically somewhat different development in certain fishes.

In Amia the so-called basisphenoids are described by Bridge (No. 7, p. 613) as "two small osseous nodules," one on each side of the head, "resting upon and in part imbedded in the

cartilaginous, anterior clinoid wall." From the position of these nodules Bridge was led to conclude that they were probably ossifications that commenced in the strong fibrous membranes that close the optic fenestrae of the fish, and that they subsequently invaded the anterior clinoid wall. They were homologized by him, under some reserve, with the "pre-pituitary portion of the basisphenoid of other fishes"; but as there is, in fishes, no postpituitary portion of this bone, so far as I can find described, the portion of the bone so specifically defined by Bridge must have been intended to include the entire bone. With this conclusion, as applied to the entire bone of teleosts, Sagemehl entirely agrees, the principal reason given by him being that if the bones are not the homologues of the teleostean basisphenoid they would become ossifications peculiar to Amia alone, among all fishes (No. 25, p. 215). The disappearance of the wide cartilaginous bar that separates the two bones in Amia, and their subsequent fusion into the single impair bone of teleosts, is said by Sagemehl to be brought about by the compressive action of the additional recti muscles, which, in the latter fishes, find their way into the eye-muscle canal.

In my own earlier work on Amia I was led to strongly doubt this homology of the so-called basisphenoids of that fish with the teleostean basisphenoid. Later work, and a more special study of the region, convince me that it is wholly wrong, as is also the supposed homology of the teleostean basisphenoid with the similarly named bone of higher vertebrates.

In my earlier work (No. 2, pp. 406, 407) I found the so-called basisphenoids of Amia of variable size and form, not only in different specimens, but also on the two sides of the head in the same specimen; and I found them developing in connection with the origins of three of the recti muscles. I considered them, as Bridge did, largely of membranous origin, because they lay, in the adult, lateral to the internal carotid arteries, while in larvae, those arteries, after having pierced the basis cranii, ran upward and forward on each side of the head, along the lateral surface of the ventral portion of the cartilaginous, anterior clinoid bar. The further course

of each artery, and its relation to the clinoid bar, considered at the time as unimportant, was said to be upward along the anterior surface of the dorsal edge of the bar, internal to a projecting, anterior, dorso-lateral corner of the bar, the artery not again entering the cartilage at all.

In Scomber, work being done in my laboratory here by Dr. Dewitz shows the carotid artery on each side, running upward along the anterior edge of the lateral wing of the so-called basisphenoid of that fish. In Salmo it apparently has a similar course (No. 20, Pl. V, Fig. 7). The artery in Scomber and Salmo thus has exactly the same relation to the basisphenoid bone that it has in Amia to the cartilaginous, anterior clinoid bar.

Why, then, should the cartilaginous, anterior clinoid bar of Amia not be the unossified homologue of the basisphenoid bone of Scomber and other teleosts? It fulfills exactly all the conditions required; the otherwise perplexing difference in the relations of the internal carotids to the so-called basisphenoids in Amia and Scomber are naturally explained; and Amia would not differ from all other ganoids in possessing osseous rudiments of a basisphenoid, as Bridge was forced to assert (No. 7, p. 614). If such be the case the homologues of the two bones that cap the bar in Amia must be looked for elsewhere than in the teleostean basisphenoid. I consider each of them as a part of the orbitosphenoid of its side of the head, ossified from an independent center and not fused with the rest of the bone because of the great development of the optic fenestra. In support of this proposition it is to be noted that, in their general position, and especially in their relations to the internal carotid arteries, the two bones of Amia agree closely with the anterior clinoid processes of the orbitosphenoid part of the sphenoid bone of man; and that the orbitosphenoid in man must necessarily ossify from two different centers in those cases in which the presphenoid bone develops, as Thane says it sometimes does, independently of the pair of nuclei that first appear on the inner sides of the optic foramina (No. 24, vol. ii, pt. i, p. 76).

In fishes I can find no recorded instance of such a development of the orbitosphenoid from two centers, nor of a second-

ary separation of the bone into two parts by the optic fenestra. The bone is, however, a variable and inconstant element of the piscine skull. It may be wanting ; may be preformed in cartilage (Amia), or in membrane only (No. 32, p. 255) ; may be fused with its fellow of the opposite side of the head (No. 27, p. 68) ; and may be, as in Polypterus, fused also with both the alisphenoids and the teleostean basisphenoid to form a single impair bone, called by Traquair (No. 31, p. 170) the sphenoid bone, and by Pollard (No. 23), the orbitosphenoid. In Traquair's figures (Figs. 2, 3) the bone seems even to extend backward beyond and around the pituitary fossa. In Pollard's figures (Fig. 12), taken perhaps from a younger specimen, it does not extend so far.

Where the orbitosphenoid, in fishes, is found impair, and the cartilage of the interorbital part of the basis cranii has not disappeared, as in Polypterus and certain of the Characinidae, the median part of the bone lies on the dorsal surface of the cartilage, and is not seen from the outer ventral surface of the skull (No. 31, p. 170, and No. 27, Figures).

These facts all seem to indicate that the orbitosphenoids and so-called basisphenoids, once having appeared in any fish, as ossifications preformed either in cartilage or in membrane, can extend themselves in all directions, not only in the contiguous or adjacent cartilage but also, and by preference, in the membranes that line the optic and pituitary parts of the skull, and fill its orbital and interorbital openings. The same would seem to be true of other vertebrates also, for in man the orbitosphenoids of opposite sides of the head, in their later development, send, according to Sutton (No. 29, p. 582), "a thin lamella across that portion of the presphenoid which is anterior to the optic groove, thus excluding it from the cranial cavity." As the presphenoid first appears, according to Sutton, "on the deep aspect of the perichondrium," these thin lamellae of the orbitosphenoid must necessarily lie entirely superficial to the subjacent cartilage. Moreover, the sphenoid bone in man is subject to certain variations (No. 24, vol. ii, pt. i, p. 47) which are further important indications in this connection. A middle clinoid process is often found, sometimes connected by

a spiculum of bone to the anterior clinoid process, thus forming a foramen for the carotid artery, the carotico-clinoid foramen, which is strikingly similar to the carotid canal of my descriptions of Amia. The anterior and posterior clinoid processes may be similarly united by a spiculum of bone, which thus replaces a part of the thick glistening membrane of Amia ; and the petro-sphenoidal ligament may be ossified, thus forming a foramen through which the inferior petrosal sinus and the sixth nerve pass (No. 24, vol. ii, pt. i, p. 43), bone thus again replacing parts of the membrane of Amia. This membrane in Amia accordingly deserves more attention than has heretofore been given it.

The cranial cavity of fishes is said by Sagemehl (No. 26) to be filled with a mass of *Fettgewebe* or *Schleimgewebe*, usually voluminous, which occupies the entire space between the inner surface of the skull and a single vascular membrane which is closely applied to the outer surface of the brain. The outer and inner surfaces of this tissue are partially differentiated as limiting membranes, and between the inner of these membranes and the vascular membrane there is a slit-like pericerebral lymph space, which Sagemehl considers as the homologue of the subdural space of higher vertebrates. The single vascular membrane is accordingly considered by him as the pia mater and arachnoid together of higher vertebrates ; the voluminous mass of fatty or *Schleim* tissue, as the dura mater.

The outer, partially differentiated limiting membrane of the dura mater, so defined, is said by Sagemehl to be closely applied to the entire inner surface of the skull, excepting only the labyrinth recesses, and to be the periosteum or perichondrium, as the case may be, of the cranial cavity. It can be separated into two layers, the outer of which, alone, is the osteoblastic layer of the membrane, the inner layer being of a fibrous character.

In the spinal canal the outer limiting membrane of the cranial dura mater seems, from Sagemehl's descriptions, to be separated, as a separate membrane, from the rest of the dura mater ; for he says that the spinal dura mater does not lie, as the cranial dura mater does, against the inner surface of the

enclosing bone and cartilage, but is separated from that surface by a tough, fibrous membrane, which is the internal periosteum of the vertebral column. The dura mater lies inside this membrane, separated from it by an epidural space, and its external surface is simply a hardened superficial portion of the general tissue of the structure, and not at all the partially differentiated and partly osteoblastic limiting membrane of the cranial dura mater. The spinal and cranial durae are thus, from Sagemehl's own descriptions, not exactly similar structures, notwithstanding his definite statement to the contrary (No. 27, p. 470). It is perhaps not unimportant in this connection to note that fibrous bands, the interclinoid ligaments, are normally found beneath the dura mater in the pituitary region of the human skull (No. 24, vol. ii, pt. i, p. 47); and that the cranial dura mater, in many vertebrates, is subject to ossification, sometimes extensive (No. 24, vol. iii, pt. i, p. 183, and No. 27, p. 85), which does not occur, so far as I find recorded, in the spinal dura.

If now the skull of Amia be considered, we find a tough, glistening, fibrous membrane which forms the floor and sides of the interorbital and pituitary parts of the cranial cavity, closing at the same time the optic fenestrae, and forming the roof of the ventral portion of the eye-muscle canal, and the median walls of its upper, lateral chambers. The hind edge of this membrane is attached to the anterior bounding ridges of the labyrinth recesses, and, between those recesses, to the front edges of the median, horizontal processes of the petrosals. A separate and independent perichondrial or periosteal membrane, the histological character of which I have not attempted to investigate, lines the floor of the eye-muscle canal, and the lateral walls of its upper, lateral chambers. That this latter membrane is not simply a reflexed portion of the outer pericranial membrane seems to be sufficiently indicated by the fibrous tufts in which the free cartilaginous edges of the orbital opening of the eye-muscle canal are always seen to end in sections of larvae of Amia. Moreover, what is exceedingly important in this connection, a subpituitary or peripituitary canal is found in Lepidosteus entirely closed, toward

the orbits as well as elsewhere, by membrane (No. 27, p. 86). In this closed canal of Lepidosteus, which is considered by Sagemehl, as it unquestionably is, as the homologue of the apparently open eye-muscle canal of Amia, fatty tissue is found, similar, undoubtedly, to the fatty tissue found both in the apparently open canal and in the cranial cavity proper of Amia.

The eye-muscle canal in Amia and Lepidosteus, and hence probably in all fishes, is thus an intracranial space, opened secondarily toward the orbits, Lepidosteus presenting the primary condition of the canal in all fishes, and not a secondary one, as Sagemehl was led to conclude. It is also, according to Sagemehl's definitions of the cranial membranes, an intradural space, notwithstanding his indirect statement that it is extradural (No. 27, p. 87); and as it gives passage, in Amia, to certain nerves and arterial and venous vessels and lodges the Gasserian ganglion (No. 2), it is a space similar to, if not strictly homologous to, the cerebral sinuses and the cavum Meckelii of human anatomy. It is, however, in Amia, a space that certainly lies morphologically in, and not internal to, the membranous bounding walls of the primordial skull. It must accordingly lie in or external to, and not internal to, the cranial homologue of those extradural fibrous tissues of Sagemehl's descriptions that line the inner surface of the spinal canal of fishes. This is all sufficiently evident from Parker's statement (No. 20, p. 131) that in salmon larvae the membranous, interorbital cranial walls, later ossified as the orbitosphenoids, "pass down into the interorbital septum, which is continuous below the perichondrium of the tilted and coalesced trabeculae"; and Studnička's statement (No. 30, p. 618) that the membranous brain capsule of Ammocoetes "sich dorsal an die Trabeculae ansetzt."

The fatty tissue found in the eye-muscle canal, both in Amia and Lepidosteus, is then presumably similar, in general character, to that found in the membranous brain capsule of the Cyclostomata (No. 30), and naturally subject to chondrofication, as in those fishes, and hence to subsequent or independent ossification. Such being the case the eye-muscle canal in different fishes, and the corresponding space in other verte-

brates as well, is naturally subject to much variation in form and size, according to the extent and manner in which its membranous walls adhere to each other and are chondrofied or ossified.

Further important evidence in support of these several conclusions is found in Jacoby's statement (No. 16, p. 81) that a certain dorsal process of the cartilaginous orbitosphenoid of human embryos indicates an earlier cartilaginous connection of the orbitosphenoids with the *Parietalplatten;* cartilage thus taking the place, in the early ancestors of man, of the thick, so-called dural membrane of Amia. In those early ancestors the alisphenoids must necessarily have been excluded from the bounding side walls of the cranial cavity proper, as they are in Amia.

The orbital and interorbital openings of the skull of fishes must now be considered.

The optic fenestra of Sagemehl's descriptions is considered by him as an enlargement of the foramen by which the optic nerve, on each side of the head, pierces the side wall of the skull (No. 25, p. 202). In the fresh skull this opening, in Amia, consists of two parts, one of which is closed by the anterior portion of the tough, fibrous dural membrane, which here forms a part of the side wall of the skull, while the other part of the opening is apparently open to the orbit and is the tall orbital opening of the eye-muscle canal of my descriptions. The posterior portion of the tough fibrous membrane lies inside the skull, internal to the alisphenoid, and is not exposed to the outer surface.

The optic nerve and the arteria ophthalmica pierce the anterior, exposed portion of the tough fibrous membrane, and enter the orbit at once. The other nerves that pierce the membrane pierce it in its posterior portion, or in the limiting region between its two portions, and enter the eye-muscle canal, from which they issue, by the orbital opening of the canal, into the orbit. The vena ophthalmica and the external rectus muscle, which enter the eye-muscle canal from the orbit by the orbital opening of the canal, do not pierce the tough, fibrous membrane at all.

There are thus in the recent state of Amia two morphologically distinct openings fused to form the single fenestra of Sagemehl's descriptions of the prepared skull. The same is true of all teleosts that I find described, but the conditions are there less obvious than in Amia. Moreover, in those teleosts in which the interorbital part of the skull is reduced to an impair interorbital septum, another opening is, or may be, added to the two optic fenestrae of Amia; the orbital region of the prepared skull of such fishes presenting three openings, two of which are lateral and one median. This is evident in Sagemehl's descriptions of Macrodon (No. 27, p. 67), and in the sectional view given by him of the orbital part of the skull of Erythrinus (No. 27, Pl. I, Fig. 8). The two lateral openings lead from orbit to orbit, and include, in their anterior portions, those perforations of the interorbital wall or septum that are said to be formed around the optic foramina. In their posterior portions they contain the orbital openings of the eye-muscle canal. The median opening lies between the postero-superior margins of the lateral openings and leads directly from the orbits into the cranial cavity. The flatter the hind wall of the orbit, and the larger the interorbital perforation, the more separate and distinct does the median opening of the brain case become, as Brooks' side view of the skull of the haddock plainly indicates (No. 8, Pl. V, Fig. 1). The lateral openings are the optic fenestrae as defined by Sagemehl; the median opening, wrongly called by him the optic fenestra in Macrodon, may be called the orbital opening of the brain case, or simply the orbital fontanelle. The optic fenestrae of Sagemehl are apparently the orbito-sphenoidal fenestrae of Parker's descriptions of Lepidosteus (No. 21, p. 480).

The optic fenestrae of teleosts, as above defined, are, in the fresh skull, entirely closed by membrane, excepting in their ventro-posterior portion, where the membrane on each side of the head is interrupted by the orbital opening of the eye-muscle canal. The anterior or antero-ventral part of the membrane of each side is, in those fishes in which a median, interorbital septum is found, fused with the corresponding part of the membrane of the opposite side to form that septum. The dorso-posterior

portion of the membrane of each side closes, in such cases, the corresponding half of the orbital fontanelle. Where there is an interorbital septum and no teleostean basisphenoid bone, as in the Characinidae and Cyprinidae, the membranes of opposite sides unite in their mid-ventral portion and are continued backward to form the membranous basisphenoid and the pituitary fossa, forming at the same time the floor of the cranial cavity and the roof of the eye-muscle canal. The orbital opening of the latter canal thus lies external to, and inferior to, this part of the membrane. This is all evident in itself from Brooks' and Sagemehl's several descriptions and statements, and is practically shown to be the case in one of Vrolik's figures of Esox lucius (No. 32, Fig. 9).

Through the orbital fontanelle, as above defined, the optic nerves are said by Sagemehl to issue, in all the teleosts described by him (No. 27, p. 70, and No. 28, p. 570). The nervus oculomotorius on each side is said by him to issue through the same opening, or through a special foramen in that part of the petrosal that lies lateral to, and in front of, the pituitary fossa. The trochlearis issues through the fontanelle in Cobitis and its related species, but in all the other fishes described it pierces the alisphenoid by a small foramen, the exact position of which is not given.

Each half of the orbital fontanelle in certain of these fishes thus corresponds exactly, in the structures it transmits, the optic nerve alone excepted, to the dorsal part of the tall orbital opening of the eye-muscle canal of Amia. In the other fishes described, it differs only in that the trochlearis and oculomotorius have become enclosed in the edges of the bones that bound the opening. In none of the fishes described is there an upper lateral chamber of the eye-muscle canal as in Amia.

The arrangement and disposition of the parts here under consideration thus indicate that that part of the internal fibrous layer of the external limiting membrane of the dura mater of Sagemehl's definitions that forms on each side of the head of Amia the median wall of the upper lateral chamber of the eye-muscle canal has, in all the teleosts described by Sagemehl, fused more or less completely with that subjacent, external,

perichondrial or periosteal layer of the same membrane, which in Amia forms a separate and independent lining of the inner surface of the lateral wall of the chamber. The dorsal portion of the tall orbital opening of the eye-muscle of Amia is thus, in these teleosts, closed toward the orbit; and the upper lateral chamber of the eye-muscle canal on each side of the head is reduced to certain intradural spaces, or to certain canals or chambers which traverse, or lie in, the side wall of the skull, and transmit the several nerves. The same is apparently true not only of all other teleosts, but also of all elasmobranchs, as the membranous interorbital walls of Chimaera and Callorhynchus plainly show (No. 13, Figs. 1, 2).

The two separate layers of the dural membrane of Amia having fused in other fishes, or never having separated to the extent found in Amia, whichever it may be, chondrification or ossification invades them from different sides and to different extents in different fishes.

In most teleosts the petrosal in particular undergoes a great development, often extending forward in the dural membrane, and also in the adjoining cartilage of the side wall of the skull, beyond the lateral edge of the pituitary fossa to the hind wall of the orbit, a part of which it forms. This marked characteristic of the teleostean skull, found already indicated in Amia, is accompanied by a relatively small development of the alisphenoid, that bone in teleosts seeming never to invade the dural membranes or adjacent cartilage to any great extent. The teleostean basisphenoid, where it is developed, also extends its horizontal wings on each side in the dural membrane, invading that part of the membrane that lies in front of the pituitary fossa, and even reaching and articulating with the anterior extension of the petrosal, or with the adjacent ventral edge of the alisphenoid. Esox represents an intermediate stage in this development (No. 32, Pl. XVIII, Fig. 9).

In Polypterus, in marked distinction to Amia and teleosts, it is the alisphenoid and not a petrosal bone that tends to occupy that antelabyrinthian region of the skull that lies between the trigeminal and facial foramina. In man, the complete invasion of this region by the former bone is plainly shown by a com-

parison of Jacoby's figures and descriptions of human embryos (No. 16) with the conditions found in the adult. Gegenbaur is even said by Jacoby (No. 16, p. 81) to have characterized the great development of an alisphenoid bone as a peculiarity of man.

In this invasion of the sphenoidal region of the skull by different ossifications, whether in fishes or in man, the relations of the nerves issuing to the several bones, as found in Amia, remain remarkably constant.

In teleosts, the opticus issues in front of or above the cartilaginous, membranous, or osseous basisphenoid, between it and the orbitosphenoid. The oculomotorius remains always in front of the alisphenoid, but may become enclosed in the anterior edge of the anterior extension of the petrosal. The trochlearis lies in front of the alisphenoid, or may become enclosed in the anterior edge of that bone. The profundus cannot be recognized in Sagemehl's descriptions of any of the fishes examined by him. In the haddock (No. 8, p. 171), what seems to be the nerve issues in front of the alisphenoid; and in Amiurus (No. 19, p. 275, and No. 34, p. 366), through the alisphenoid near that edge of the bone that articulates with the basisphenoid. The trigeminus in the Characinidae (No. 27, p. 70) issues through a single foramen in the anterior orbital part of the petrosal, its relation to the alisphenoid thus being uncertain. In the Cyprinidae, the ophthalmic branch of the trigeminus issues through a special foramen in the alisphenoid (No. 28, p. 568), the maxillary branches of the nerve issuing through a foramen which lies partly in the petrosal, and partly between that bone and the alisphenoid. In Leuciscina and Abramidina, the latter foramen is often separated into two parts by a bridge of bone; the upper part of the foramen, in such cases, transmitting the trigeminal nerves, and the lower part the vena ophthalmica. In the haddock and in Amiurus, the trigeminus issues with the facialis through a large foramen between the adjoining edges of the alisphenoid and petrosal, the foramen being often incompletely separated into two or more parts by bony spicules.

In man (No. 25, vol. ii, pt. i, p. 80), the opticus issues between the orbitosphenoid and presphenoid; the oculomotorius,

trochlearis, and abducens nerves, and the ophthalmic division of the trigeminus, the probable homologue of the profundus (No. 2, p. 000) issue through the sphenoidal fissure, between the orbitosphenoid and alisphenoid; the superior maxillary division of the trigeminus issues through the foramen rotundum, said by Thane to be cut off from the sphenoidal fissure, but from Jacoby's descriptions (No. 16, p. 67), lying apparently posterior to the alisphenoid; and the inferior maxillary division of the trigeminus issues through the foramen ovale, which is cut off from the foramen lacerum, which lies between the alisphenoid and periotic.

The sphenoidal fissure of man was shown in my earlier work (No. 2, p. 000) to agree strikingly in position and function with the tall orbital opening of the eye-muscle canal of Amia, and to be apparently the homologue of that opening. It is accordingly also, in whole or in part, the apparent homologue of one-half of the orbital fontanelle of teleosts.

In mammals, each half of the orbital fontanelle of fishes seems to be represented in a large opening, closed by membrane, which lies, according to Sternberg (No. 3, p. 147), between the two sphenoid bones and transmits the orbital nerves and vessels. The canalis craniopharyngeus lateralis of Sternberg, found in man and many mammals, is then the last remnant of the ventral part only of the tall orbital opening of Amia, and not a last remnant of the entire opening, as Bardeleben's statement of Sternberg's conclusions seems to indicate.

The petrosal bone, which lies in man posterior to the sphenoidal region of the skull, but which in fishes may, as shown above, invade that region to a considerable extent, and the facial nerve, which should lie morphologically in front of the petrosal, if that bone lies between successive segmental nerves, as its position in Amia seems to indicate, must now be considered.

The facial nerve in man leaves the primordial cranium, according to Vrolik, by the hiatus Fallopii and not by the stylomastoid foramen (No. 32, p. 308). This statement is based on the fact that in human embryos of from 12 cm. to 15 cm. in length, the nerve lies, after issuing from the hiatus, in a groove in the cartilage of the under surface of the skull (No. 32,

p. 307). It reaches that under surface, so far as can be judged from the figures and descriptions, through a large opening, which must be the foramen lacerum medium of the adult. Jacoby's figures and descriptions (No. 16) of a much younger embryo seem to confirm this. Vrolik's figures show little or no indication of a division of this opening into two parts by the lingula. Jacoby's figures, on the contrary, show the lower end of the opening cut off as a separate foramen by a strong cartilaginous bridge. The upper part of the opening in Jacoby's figures is simply a wide cleft in the cartilaginous side wall of the cranium, which transmits the third branch of the trigeminus, and apparently the second branch also. The ventral, completely separated, part of the cleft transmits the internal carotid artery, and is called by Jacoby in one place the canalis caroticus, and in another the foramen lacerum anterius (No. 16, pp. 66, 74). That it is not the foramen lacerum anterius of Thane's descriptions (No. 24, vol. ii, pt. i, p. 70) is sufficiently evident to need no comment.

In the adult man, the facial nerve does not traverse the foramen lacerum as it seems to in embryos. It is, however, still exposed to that foramen at the hiatus Fallopii, and, coming from the hiatus, the large superficial petrosal nerve crosses the foramen to reach the posterior orifice of the Vidian canal (No. 24, vol. ii, pt. i, p. 70), which it traverses with a branch of the external carotid artery. By the inner part of the foramen the internal carotid artery enters the cranial cavity, its groove being partially, and sometimes completely, separated from the rest of the foramen by the lingula (No. 24, vol. ii, pt. i, p. 70). The foramen spinosum and foramen ovale, both of which are cut off from the foramen lacerum, and may be, even in the adult, incompletely separated from it, transmit respectively the large and small meningeal arteries (No. 24, vol. ii, pt. i, pp. 47, 80). An irregular cleft, the petro-basilar fissure, extends from the foramen lacerum backward and outward to the jugular foramen (No. 24, vol. ii, pt. i, p. 68).

In Amia (No. 2, p. 000), the facial foramen perforates the petrosal and transmits both the facial nerve and the jugular vein. The facial nerve does not, however, leave the cranial

cavity proper by this foramen. After its exit from the brain it pierces a mesial membranous part of the anterior wall of the labyrinth recess, enters the upper lateral chamber of the eye-muscle canal, where it traverses the trigemino-facial ganglion, and then issues from the skull by the large facial foramen. Slightly below this foramen, and hence what would be in the human skull mesial to it, are the external carotid foramen and the external orifice of the internal carotid canal. Internal to the foramen, in the upper lateral chamber of the eye-muscle canal, the palatine branch of the facialis enters the posterior orifice of a canal, called in my descriptions the palatine canal, which runs forward between the parasphenoid and the ventral surface of the chondrocranium.

It is thus evident that but for the fact that the main external carotid artery of Amia enters the upper, lateral chamber of the eye-muscle canal, while in man its meningeal branches only enter the skull, there would be a striking functional resemblance between the facial and carotid foramina united, of Amia, and the foramen lacerum and jugular foramen together, of man. Moreover, that the difference in the course of the external carotid in the adult of Amia and of man is probably not of morphological importance, is evident from the fact that in embryos of the higher vertebrates (No. 27, p. 66) the external carotids have an intracranial course. Furthermore, what may possibly be related to that early condition, an external carotid may be, in rare cases, wanting even in the adult man (No. 24, vol. ii, pt. ii, p. 393).

In teleosts the same general relations of the parts here under consideration are found as in Amia, but there is great variation in the details of the disposition of the several parts, and the resemblances to the conditions found in man are not so striking as in Amia. The jugular foramen may become either partly or entirely separated from the facial foramen; the two carotid arteries may enter the eye-muscle canal by a single foramen, corresponding in position to the internal carotid foramen of Amia; and the facialis may have its exit by two foramina instead of by one (No. 27, p. 65, and No. 28, p. 559).

The trigemino-facial ganglion in Amia lies in the upper,

lateral chamber of the eye-muscle canal, the profundus ganglion in the orbital opening of that chamber. The ganglia are therefore both intradural in position, as the trigeminal ganglion is in man (No. 24, vol. iii, pt. ii, p. 234). The trigemino-facial ganglion lies in Amia immediately in front of the anterior bounding wall of the labyrinth recess and would lie on the dorsal surface of that wall if the hind end of the skull were flexed downward as it is in man. The anterior wall of the labyrinth recess is partly ossified as the petrosal. The upper, lateral chamber of the eye-muscle canal of Amia is thus both functionally and in position the equivalent, if not the homologue, of the cavum Meckelii of man.

In teleosts the *Wurzelganglien des Trigeminus* lie, according to Sagemehl (No. 26, p. 463), in the fatty portion of the dura mater, between the outer and inner limiting membranes of that structure. If the ganglia so defined form or belong to the Gasserian ganglion, that ganglion in teleosts occupies a position markedly different from what I find in Amia.

In other fishes parts of the trigemino-facial ganglionic complex may lie in canals in the side wall of the skull, and parts of it entirely outside the skull, as in Chimaera (No. 9), Laemargus (No. 10), and Acipenser (No. 12). In Necturus (No. 17) the several ganglia lie entirely outside the skull. Whether in these several cases, and in other similar ones, the ganglia are morphologically different in position from what they are in Amia, or not, depends entirely upon the positions of the two layers of the dura mater, and not upon the relations of the ganglia to the side walls of the skull. Unfortunately, the relations of the dura mater and its different layers to the ganglia are not given in any of the descriptions that I find.

The internal auditory meatus, the internal orifice of the canal by which the facial nerve in man leaves the cranial cavity, lies, according to Thane (No. 24, vol. ii, pt. i, p. 75), between the proötic and opisthotic portions of the petrous portion of the temporal bone. The proötic lies above the meatus, the opisthotic below it. The facialis in man, in that part of its course that traverses the side wall of the primordial cranium, cannot accordingly be considered as lying, in any

way, morphologically anterior to the proötic element of the temporal bone. If not simply ventral to that element it must lie morphologically posterior to it.

The petrosal, the supposed piscine homologue of the mammalian proötic, is, in Amia, a nearly circular bone, the front edge of which forms, according to Sagemehl (No. 25, p. 205), the anterior limit of the labyrinth region of the skull, notwithstanding the fact that the bone extends forward, as Sagemehl himself states, slightly beyond the anterior limiting ridge of the labyrinth recess. If Sagemehl's figures and my own (No. 2, Fig. 2) be examined it will be seen that the ridge here referred to runs from behind upward and forward across the inner surface of the petrosal, between the labyrinth recess and the upper, lateral chamber of the eye-muscle canal, and that the several foramina that perforate the bone all lie in front of the ridge. A similar but much less developed ridge is found in the Characinidae and Cyprinidae. That part of the petrosal that takes part in the formation of the labyrinth region of the skull in these fishes thus lies in marked distinction to the relation found in man, most decidedly posterior, instead of anterior, to the nervus facialis; and if the hind end of the skull in these fishes were to be flexed downward, as it is in man, so that the foramen magnum would come to lie on its ventral surface, the petrosal would necessarily lie ventral to the facialis, as the opisthotic does in man, and not dorsal to it as the proötic should.

Is then the petrosal of fishes the homologue of the opisthotic of man and not of the proötic? It certainly does not lie over the superior-semicircular canal, the place assigned to the proötic by Thane in man (No. 24, vol. ii, pt. i, p. 75); nor does it form simply the fore edge of the periotic capsule, the place assigned to the bone by Parker in fishes (No. 20, p. 96); and it is the only bone in Amia that has any relation whatever to the ampulla of either the anterior or the posterior semicircular canals, the positions assigned respectively in fishes to the sphenotic and opisthotic. Of these two latter bones it could only be the opisthotic, the term sphenotic having been introduced by Parker for the postorbital ossification.

The intercalar of fishes, which is usually considered as the homologue of the opisthotic of higher animals, is certainly not that element of the skull, for it has in Amia (No. 2), contrary to Sagemehl's statement, and as Vrolik has already shown for teleosts (No. 32, p. 285), no primary relation whatever to the periotic capsule. The occipitale laterale, the only other bone in Amia that could be the opisthotic, is also not that element, since, in Amia, it is strictly confined, in its early development, to the postauditory region of the skull (No. 2).

Moreover, the bone that lies in Polypterus between the facial and vagus foramina, that is, in the position relative to those nerves that the petrosal has in Amia, is called by Traquair the opisthotic, and considered by him as that element of the skull fused with the epiotic (No. 31, p. 168). In Lepidosteus also the bone identified by Parker as the opisthotic has a similar position, and is similarly but less completely fused with the epiotic. In Polypterus there is no proötic bone. In Lepidosteus the proötic lies in front of the facial foramen (No. 21, Pl. XXXVIII, Figs. 1, 2), as it does also in the sturgeon (No. 22, p. 176). In Menobranchus the proötic occupies a similar position, the opisthotic lying, as in both Polypterus and Lepidosteus, posterior to the facialis, fused with the epiotic (No. 15, p. 188, and Pl. XXIX, Fig. 1). In Menobranchus no sphenotic bone is given. In Lepidosteus it is shown lying dorsolateral to the proötic, and is, in the oldest stage given, almost continuous with that bone. In Polypterus the postfrontal of Traquair is traversed by the lateral canals (No. 31, p. 181), and is therefore not the homologue of the postorbital ossification alone of Amia. The bone, whatever it may be, is firmly connected by suture with the parasphenoid, but is widely separated by cartilage from the opisthotic.

If, then, the petrosal of Amia is the homologue of the opisthotic, as its general relations to the facial nerve and the periotic capsule seem to indicate, the postorbital ossification, which is usually considered as the sphenotic, must in all probability be the homologue of the proötic. This ossification in Amia forms no part of the labyrinth recess. In many teleosts, on the contrary (No. 32, pp. 278–285), it lies above

the anterior end of the anterior semicircular canal, and forms the anterior boundary of the labyrinth recess, thus occupying exactly the place assigned by Thane to the proötic in man, and by Parker to the same bone in fishes. It adjoins anteriorly the hind edge of the alisphenoid, as it should; it lies inferior to the anterior end of the squamosal, as it also should; and it is the only primary bone of the skull of Amia that has any direct relation whatever to the spiracular canal, the homologue, according to Wright (No. 35, pp. 479, 488, 492), of the canalis tubo-tympanicus of higher vertebrates, from which the Eustachian tube develops.

The sphenotic nuclei of the sphenoid bone of man are said by Sutton (No. 29, p. 580) to arise, after the appearance of the alisphenoidal and basisphenoidal nuclei, as "earthy spots in the lingulae," and they alone of all the nuclei of the bone are so specifically characterized by him. According to Thane (No. 24, vol. ii, pt. i, p. 76) they form not only the lingulae, but also the adjoining parts of the carotid grooves. The corresponding regions in the skull of Amia and teleosts are occupied by the parasphenoid. My work accordingly leads me to accept Huxley's and Parker's conclusions that "the basitemporal rudiments of the parasphenoid" of Sauropsida are the homologues of the lingulae of man (quoted No. 29, p. 584), rather than Sutton's conclusion that the homologues of the latter bones are found in the sphenotics not only of Sauropsida, but also of fishes (No. 29, p. 585).

The postorbital ossification of Amia and other fishes, although universally called either the postfrontal or the sphenotic, must not be confounded with the postfrontal bone of Reptilia, which is, according to Parker (No. 20, p. 96) and Brooks (No. 8, p. 171), simply a membrane bone, the homologue doubtless of the postfrontal bone of my descriptions of Amia, or of that bone and one or more of the postorbital bones combined. The reptilian postfrontal is said by Bardeleben (No. 4) to be represented in man by the suprasquamosal or epipteric bone.

But one bone now remains to be considered, — the basisphenoid.

The basisphenoidal part of the sphenoid bone of man forms the floor and the anterior and posterior walls of the pituitary fossa. The corresponding parts of the skull of Amia are occupied by that part of the eye-muscle canal that lies immediately below the membranous sac that forms the pituitary fossa. The floor of this part of the canal is formed by a median portion of the dorsal surface of the parasphenoid, and by cartilaginous parts of the primordial cranium that are covered externally by the lateral portions of the parasphenoid. In teleosts the corresponding part of the skull is formed by the petrosals and parasphenoid, the petrosals invading and replacing almost entirely the cartilaginous parts of Amia. The teleostean basisphenoid lies in front of this region, in the place occupied by the presphenoid bone in man.

The parasphenoid of fishes and Amphibia is said by Huxley (No. 14, p. 27) to replace functionally the basisphenoid and presphenoid of higher vertebrates, and to become, in these latter animals, confounded with the basisphenoid. Parker states more definitely (No. 20, p. 138) that "in the bird, the basisphenoid borrows its ossifying center at first from the parasphenoid."

The mammalian basisphenoid bone is thus probably not developed in fishes because of the earlier development, in connection with the dentition of these latter animals, of a large parasphenoid bone which functionally replaces it. Whether the parasphenoid is developed directly from the plates that bear the teeth, by their fusion, as Sagemehl concludes (No. 27, pp. 186, 199), or independently of those plates, from the connective tissues underlying them, as Walther concludes (No. 33, pp. 67, 78), is evidently unimportant in this connection, excepting as the origin of the bone might determine or affect its ultimate more or less complete incorporation in the skull.

If then, in general summary, it be assumed that in some animal presenting in the sphenoidal region of its skull the features characteristic of Amia, the teeth that give origin, either directly or indirectly, to the parasphenoid bone no longer being needed, the bone itself begins to be replaced or absorbed by a primary ossification, the basisphenoid; that

the parasphenoid finally disappears entirely, as a separate ossification, excepting only that part of it that forms the anterior boundary of the internal carotid foramen; that the cartilaginous, anterior clinoid wall of Amia ossifies independently; that the alisphenoids instead of the petrosals invade, on each side of the head, the region between the foramina of the trigeminal and facial nerves; and that the postorbital ossification, as the hind end of the skull is flexed downward, descends onto the dorsal surface of the petrosal and fuses with it as a part of the periotic mass, — an arrangement would arise so markedly similar to that found in the human skull that the several homologies I have here sought to establish seem much more than simply probable. To definitely establish them, and to show whether the apparently interneural position of the several bones in Amia is really of vertebral significance or not, evidently still requires a wide range of careful anatomical and embryological work.

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March 24, 1897.

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